AN ECOLOGIC AND BIOGEOGRAPHIC STUDY OF A NEW TERTIARY LAND SNAIL FROM MIDEASTERN QUEENSLAND (PULMONATA: CARYODIDAE)

JOHN STANISIC

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A new fossil land snail, *Praecaryodes antiquata* gen.et sp.nov., is described from the Middle to Late Eocene deposits of the Rundle Formation, near Rockhampton, mideastern Queensland. The species is assigned to the Caryodidae. The phyletic, biogeographic and ecological implications of this discovery are discussed. The new species suggests early diversification of the Caryodidae. □*Mollusca, Caryodidae, Praecaryodes antiquata sp.nov., ecology, biogeography, Eocene, land snail.*

John Stanisic, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 14 February 1994.

Few Australian fossil land snails are known and most are from Pliocene-Pleistocene sediments of southern Australia (e.g.Strzelecki, 1845; Johnston, 1880; Ludbrook, 1978, 1984). McMichael (1968) recorded *Meracomelon lloydi* from the Carl Creek limestones of north-west Queensland and the Northern Territory; Kershaw (1988a) discussed several fossil land snails of problematic affinity from Pleistocene deposits in the Kent Group of islands, Bass Strait; and Hill et al. (1970) recorded *Pedinogyra* sp. (family Caryodidae) from a limestone quarry at Marmor, south of Rockhampton, mideastern Queensland (hereafter MEQ). The discovery of *Praecaryodes antiquata* gen.et sp.nov. in Middle to Late Eocene deposits of MEQ is a significant addition to the Australian fossil land snail fauna.

The age of the fossil and its relationships to the extant Gondwanan family Caryodidae provide a basis for biogeographic speculation about the evolution of land snails in eastern Australia. The climatic and habitat shifts which have occurred in eastern Queensland since the early Tertiary have favoured the development of dry-adapted species. This provides an ecological framework for discussing caryodid history in the region.

All material studied is in the collections of the Queensland Museum (hereafter prefixed QMF).

STRATIGRAPHY, AGE AND PALAEOENVIRONMENT

The Narrows Beds (Fig. 1), NW of Gladstone, MEQ, which include the Curlew and Rundle Formations and Worthington Beds (Henstridge and Missen, 1982) are a Tertiary non-marine sequence containing oil shale seams. These richly fossiliferous beds contain ostracods (Beasley, 1945), fish (Hills, 1943), reptile fragments (crocodile and turtle) and flora (Foster, 1979; Foster & Harris, 1981; Rowett, 1988). Freshwater gastropods (?Planorbidae) are common in some units (Coshell, 1983). The land snail remains were contained in the Claystone Unit of the Ramsay Crossing Seam within the Rundle Formation.

Little data are available to independently correlate the Tertiary Basins of central and northern Queensland and most age determinations are based on long distance correlation with Tertiary sequences in Southern Australia. It has yet to be demonstrated that the northern Australian Tertiary floras can be conveniently reconciled with known spore-pollen ranges from southeastern Australia. Given these shortcomings, the most recent age estimate of the Rundle Formation is Middle to Late Eocene (Day et al., 1983).The depositional environment of the Ramsay Crossing Seam was interpreted as shallow lacustrine with lacustrine and pedogenic phases (Coshell, 1983).

Occurrence of land snails among the predominantly freshwater fossil remains suggests that they are drift material which has been washed into the lagoon from surrounding areas. Henstridge & Missen (1982) postulated a similar mechanism to explain the high levels of carbonaceous matter among the oil shale.

Information on the contemporaneous vegetation present in the area surrounding the Rundle Formation depositional environment is not available. However, the presence of large amounts of carbonaceous material in the oil shales and the

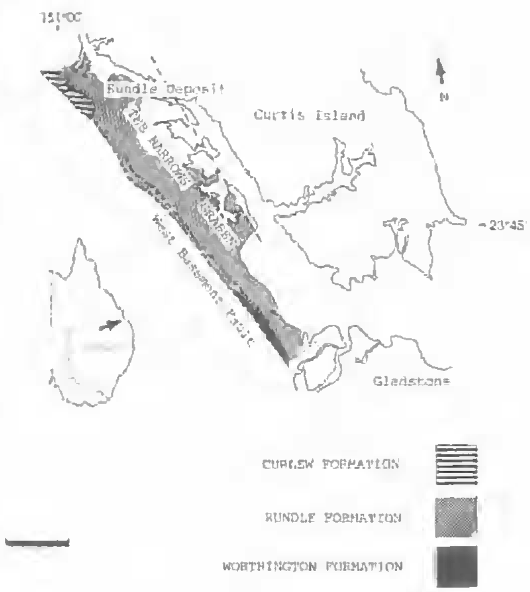

FIG. 1.Locality map showing the Rundle Deposit and the Tertiary stratigraphic units in the Narrows Group. Map adapted from Henstridge & Missen (1982). Scale line = 1km.

inference of high rainfall and humidity (Henstridge & Missen, 1982) suggest a tropical to subtropical closed forest. Fossil flora of the younger Curlew Formation indicates deposition in a low energy, freshwater swamp in an area of marginal tropical/subtropical closed forest. These interpretations correlate with a broader perspective of vegetational change in eastern Australia during the Eocene (Kemp, 1981) pointing to a widespread closed-canopy rainforest early in the epoch, becoming more restricted (i.e. replaced by sclerophyllous elements) in the Middle to Late Eocene when climate began to fluctuate.

SYSTEMATIC PALAEONTOLOGY

Family CARYODIDAE Thiele, 1926

Australian acavoid land snails have been traditionally associated with the mesurethran family Acavidae which also included a number of species from Africa, India and South America (Zilch, 1959-60). Solem (1978a) separated the Australian genera as a separate family, the Caryodidae, and placed it and the Acavidae near the more advanced sigmurethran pulmonates. Tillier (1989) rejected this arrangement in favour of a single family. Smith (1984, 1992) also preferred to consider the Australian species as a distinct family and this system is followed here.

The Caryodidae includes an unusual mix of shell types ranging from the depressedly conoidal *Anoglypta* Martens, 1860 and giant bulimoid *Hedleyella* Iredale, 1914 to the lenticular, thin-shelled *Pandofella* Iredale, 1933 and the flat-coiled, heavy-shelled *Pedinogyra* Albers, 1860. This led Iredale (1937) to place these genera in several different family units. Only thirteen extant species are known (Smith, 1992). All live in the moist forests of eastern Australia.

Praecaryodes gen.nov.

DIAGNOSIS

Shell large and subglobose with a flattened spire. Shell sculpture predominantly radial with weak spiral grooves on the body whorl. Umbilicus absent. Aperture ovate; lip thickened and reflected.

TYPE SPECIES

Praecaryodes antiquata sp.nov.

ETYMOLOGY

A combination of the Latin *prae* meaning early and the nominate genus of the family Caryodidae.

Praecaryodes antiquata sp.nov. (Figs 2-5)

MATERIAL EXAMINED

HOLOTYPE: QMF13905, Rundle, MEQ. Collected by Southern Pacific Petroleum, August, 1985.

PARATYPES: QMF13451, QMF17642, 2 specimens. Unit T claystone, Ramsay Crossing Seam, Rundle Formation, MEQ, open cut, L. Coshell.

ETYMOLOGY

Referring to the antiquity of the specimen.

DESCRIPTION

Shell large (damaged and distorted), subglobose, diameter 41.94mm with 4¾ normally coiled whorls, the last greatly expanded and not descending in front. Spire and apex flat. Height 28.30mm. Height of body whorl 21.62mm. Protoconch 2 whorls, sculptured with fine, crowded, weakly protractively sinuated radial ribs. Post nuclear sculpture of numerous, fine, protractively sinuated radial ribs, becoming

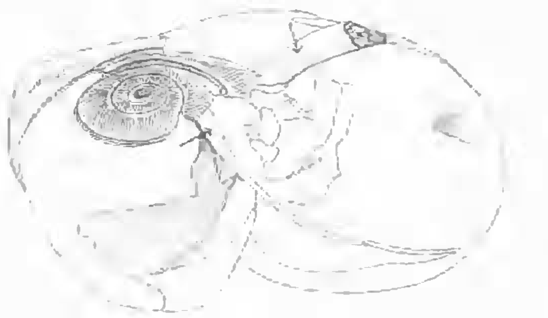

FIG. 2. *Praecaryodes antiquata* sp.nov., QMF13905, holotype. Drawing to show depressed shape and thickened lip (arrowed). [Drawing by Alison Hill].

slightly less conspicuous on the body whorl, and irregularly spaced spiral grooves which are particularly noticeable on the body whorl. Umbilicus absent. Sutures weakly impressed. Whorls flattened above and below a weakly keeled periphery. Aperture ovate. Lip strongly thickened and reflected. Columella inserted obliquely. Parietal callus obscured.

REMARKS

In spite of the small amount of the material available for study, sufficient features are present to make familial placement possible. The flattened spire, sculpture, coiling pattern, whorl expansion rate and reflected lip relate *P. antiquata* to the Caryodidae, in particular the flat-coiled *Pedinogyra*. However, the absence of an umbilicus is a major departure from this genus and indicates a possible connection with the bulimoid caryodid genera. In Tasmania a few examples of the bulimoid form do have an umbilicus and occasionally, juveniles have an umbilicus which is lost with growth. This may indicate that an umbilicus was more common in ancestral forms of these species and that the non-umbilical lineage of *Praecaryodes* is distinct from these.

Sphaerospira Mörch, 1867 (+*Figuladra* Iredale, 1933, *Varohadra* Iredale, 1933 and *Bentosites* Iredale, 1933) (family Camaenidae) have numerous species living in the rainforests of southeastern Queensland (hereafter SEQ) and MEQ (Smith, 1992). These genera also have globose to subglobose shells which often lack an umbilicus. However they have almost obsolete adult sculpture, smooth protoconch, less expanded body whorl and weakly reflected lip. *Xanthomelon* Martens, 1861 (family Camaenidae), from the drier vine thickets of eastern Queensland, has a large, globose shell without an umbilicus and with conspicuous cancellate sculpture on the body whorl. However the protoconch is smooth and most importantly, the lip is not reflected.

Biogeographically, these eastern Australian camaenids are considered to be post-Miocene northern immigrants (Bishop, 1981), hence appearing in the region much later than *P. antiquata*.

DISCUSSION

The Middle to Late Eocene age of *P. antiquata* represents a marked chronological extension of the fossil record of land snails in Australia and significantly predates previous records (Pliocene/Pleistocene). The presence of a reflected lip, a probable derived character within the Caryodidae, has important implications for the timing of the first appearance of the family on the Australian land mass.

A brief reappraisal of the relationships of extant caryodid genera is a necessary preamble to biogeographic considerations.

CARYODID RELATIONSHIPS

Caryodids have an unusually diverse array of shell form yet Dartnall & Dartnall (1972) concluded that the genera were closely related on the basis of karyotype and reproductive anatomy. Their results segregated the Tasmanian *Anoglypta* and *Caryodes* Albers, 1850 from the mainland *Pygmipanda* Iredale, 1933, *Hedleyella* and *Pedinogyra*. Two remaining mainland genera - *Brazieresta* Iredale, 1933 and *Pandofella* -were not included in their study. Kershaw (1988a,b), utilising fundamental features of shell morphology, substantially agreed with this interpretation.

The separation of *Anoglypta* and *Caryodes* from mainland caryodids is supported by protoconch features. The nuclear sculpture of the Tasmanian genera is characterised by distinct spiral cords which are irregularly and weakly cut into long segments by radial grooves (Kershaw, 1988 a,b). Mainland caryodids have more regular decussate apical sculpture. In *Brazieresta* and *Pandofella* this decussate nuclear sculpture is almost granular. These genera have thin, reduced shells and anatomical features consistent with an evolutionary move to slugdom. This may indicate a close relationship between them even though *Pandofella* has a genital diverticulum positioned similarly to that of *Anoglypta* (Stanisic, unpubl.).

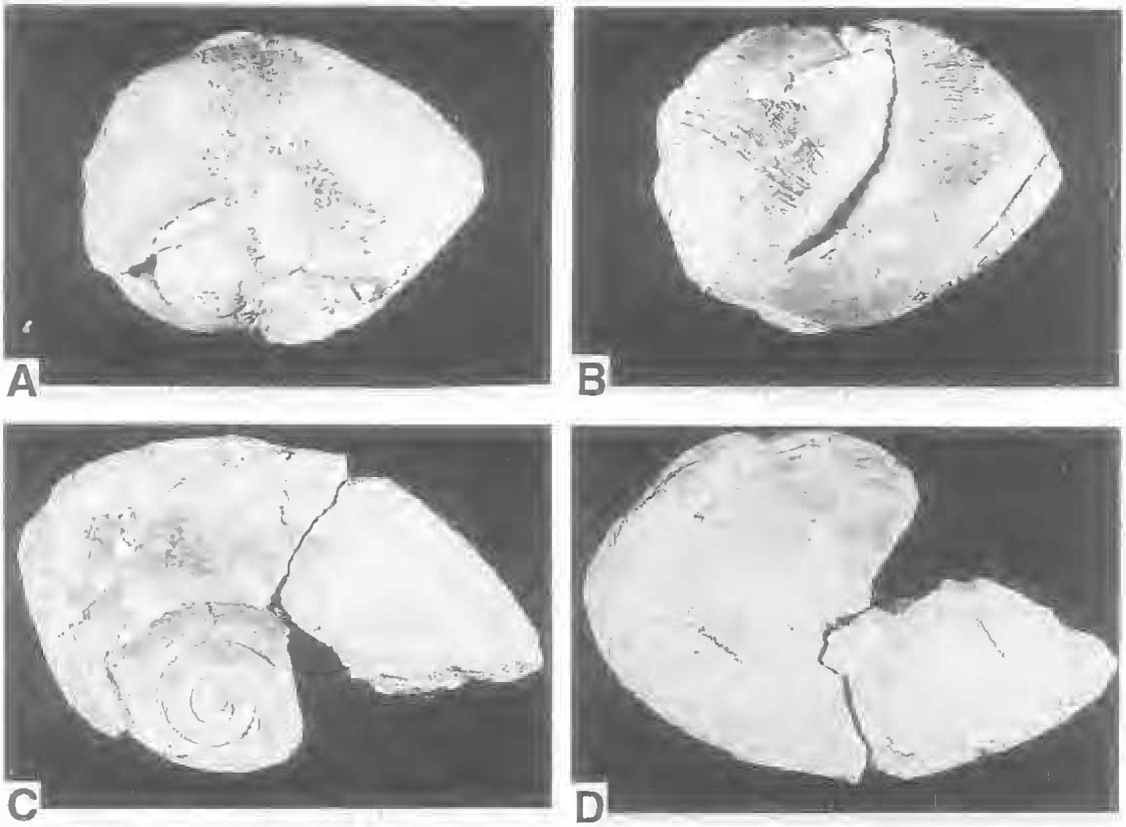

FIG. 3.*Praecaryodes antiquata* sp.nov. A-B, QMF13905, Rundle, MEQ, holotype; C-D, QMF17642, Rundle Formation, MEQ, paratype (internal cast). Scale units in mm.

Solem (1978a) showed that arrangement of internal structures in slug-like taxa were often related to spatial readjustments resulting from a reduction in the visceral hump rather than representing primary phylogenetic changes. *Brazieresta* and *Pandofella* survive in cool moist, upland refugia in northern NSW (*Brazieresta*) and MEQ respectively and possibly represent highly specialised, temperate relicts of a single (monophyletic) lineage within the family.

Pygmipanda, *Hedleyella* and *Pedinogyra*, display shell features which indicate a long period of development by each under different ecological regimes. *Pygmipanda* lives in the moist, warm to cool, temperate forests of central and southern New South Wales (NSW) and Victoria; *Hedleyella* in the warm temperate and warm humid subtropical forests of northeastern NSW and SEQ; and *Pedinogyra* in the drier araucarian microphyll vine forests and semi-evergreen vine thickets of northeastern NSW, SEQ and MEQ. Shell form indicates specialisation to different adaptive zones.The reduced sculpture, low whorl numbers, inflated body whorls and large apertures of *Hedleyella* and *Pygmipanda* are adaptations consistent with life in humid, moist forest. In contrast the heavy and flat shell of *Pedinogyra*, with small, downwardly directed aperture and higher whorl numbers is adapted for life in a dry-forest habitat.

Conchologically the position of *Pedinogyra* is the most difficult to reconcile within the caryodids. The discoid shape, wide umbilicus, heavy shell with thickened lip and strong radial apical sculpture are features which stand at odds with those of the other genera. Nonetheless, Kershaw (1988b) emphasised that *Pedinogyra* was a derived bulimoid taxon, citing the transition series within *Hedleyella* i.e. imperforate bulimiform [*H. maconelli* (Reeve, 1853)] to umbilicate, globose, sub-auriform [*H. falconeri* (Gray, 1834)] as a means of deriving a flat-coiled

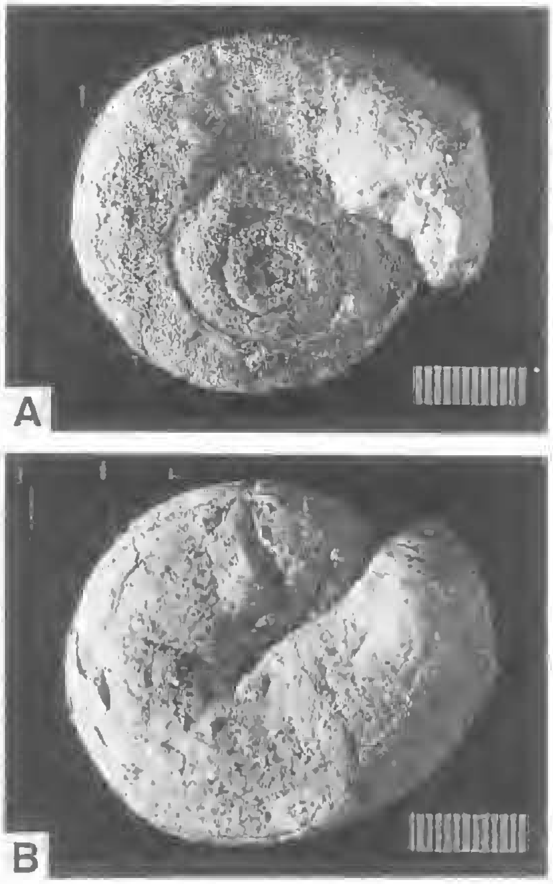

FIG. 4.*Praecaryodes antiquata* sp.nov. QMF13451, Rundle Formation, MEQ, paratype (internal cast). A, top view; B, bottom view. Scale units in mm.

shell from the more generalised bulimoid form. However, one feature of *Pedinogyra* which is not easily explained in the context of general caryodid patterns is the thickened reflected lip.

P. antiquata possesses features which are transitional between the bulimoid caryodid forms and *Pedinogyra* - a depressedly globose bulimoid shell with small aperture and thickened, reflected lip. The latter character, rare within extant forms, indicates a possible close relationship with *Pedinogyra*. *P. antiquata* may be the moist forest ancestor of these modern-day, flat-coiled caryodids.

Caryodid Fossil History

Comparatively little information is available on other caryodid fossils. Hill et al. (1970) recorded a species of *Pedinogyra* from Pleistocene limestone deposits at Marmor, south of Rockhampton, MEQ. Subfossil *Pedinogyra*, possibly Pleistocene in age are also known from the Cammoo and Olsen Caves, north of Rockhampton, MEQ (Stanisic, unpubl.). These are all considered to be conspecific with an extant species, *Pedinogyra minor* (Mousson, 1869) (=*nanna* Iredale, 1937), which lives in the region.

Kershaw (1988a) discussed a fossil land snail from the calcareous beds (?Pleistocene) of the Kent Group of islands, Bass Strait, which may be related to *Pedinogyra*. Inspection of the shell (Queen Victoria Museum, Launceston - QVM:87.G.163) reveals an overall resemblance to *Pedinogyra*. However, compared with that genus, it has fewer whorls, smaller umbilicus and vague traces of regularly spaced incised spiral lines cutting across fine radial ribs on the last ¼ whorl. The resulting cancellate pattern is not equivalent to that seen in extant caryodids but is more commonly associated with the shells of carnivorous Rhytididae. Although the peripheral keel of the Tasmanian fossil is not present in any living Australian rhytidid, it is possessed by several New Zealand species of that family.

Biogeographic Implications

The presence of a number of derived caryodid features (pronounced radial sculpture and thickened, reflected lip) in *P. antiquata* indicates that the adaptive radiation of the Caryodidae in central eastern Australia was probably completed much earlier i.e. beginning of the Tertiary or possibly Late Cretaceous. This would place familial origins contemporaneously with the emergence of the advanced, sigmurethran camaenids in northern land masses (Solem, 1978b). Hence rather than being ancestral to the helicoid sigmurethrans, the caryodids (and probably acavoids of Africa and India and South

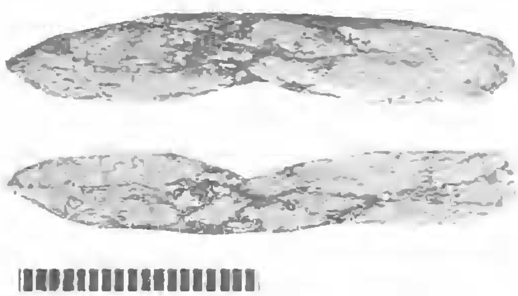

FIG. 5.*Praecaryodes antiquata* sp.nov., QMF13451, paratype. Sectioned to show internal structure. Scale units in mm.

America) may represent an equivalent and parallel level of snail evolution in southern land masses.

ECOLOGICAL IMPLICATIONS

The impetus for the initial radiation of the caryodids on the Australian land mass would have been enhanced by the significant change in the nature of the flora from one dominated by conifers to one with a significant angiosperm component at the Cretaceous/Tertiary boundary. (Kershaw et al., 1991). The switch to a broad-leaved, closed-forest with a propensity for greater leaf fall would have favoured 'moisture-loving' snails by providing a new adaptive zone of leaf litter with moist to humid micro-environments and shelter. Subsequent distribution of the family in eastern Australia would have been greatly influenced by the climatic and vegetational changes that took place in the latter part of the Tertiary and Quaternary (Kemp, 1981; Kershaw, 1981). The diversification of eastern Australian rainforest into temperate, tropical and subtropical forms had its beginning in the Mid-Eocene (Kershaw et al., 1991). With the onset of the Miocene aridity phases 'drier' subtropical rainforest developed where edaphic profiles were suitable and in the late Tertiary and Quaternary, mesothermelements in the north were confined to montane refugia.

P. antiquata lived in conditions which were wetter and cooler than MEQ today. Vegetation was dominated by *Nothofagus* forest types (Kemp, 1981), a conclusion supported by palynological evidence from the Rundle deposits (Foster, 1979). Significantly *P. antiquata* displays some shell characters (comparatively thin shell, more conspicuous sculpture) which today are found in *Pedinogyra rotabilis* (Reeve, 1852) and *P. effossa*. These species live in marginally wetter areas (Border Ranges, Conway and Clarke Ranges respectively) at the periphery of the main mass of *Pedinogyra*.

Creation of the Fitzroy dry corridor would have considerably changed conditions in the Rockhampton - St Lawrence region and although refugia in MEQ (Sarina - Proserpine) enabled caryodids to survive [*Pedinogyra effossa* Iredale, 1937; *Pandofella whitei* (Hedley, 1912)] this drastic local change in environment probably led to the extinction of *P. antiquata*. Subsequent conditions would have favoured the development and dispersal of the comparatively dry-adapted, thicker, smoother shelled *Pedinogyra hayii* (Griffith & Pidgeon, 1933) - *P. allani* Iredale, 1937 - *P. minor* in the araucarian vine forests of southeastern Queensland (with *P. minor* replacing *P. antiquata* in the drier areas of the Gladstone - Rockhampton region).

The colonising wave of northern camaenids (*Sphaerospira* s.l.) would have been able to take advantage of occasional later climatic shifts to wetter conditions and now occupy the microhabitats most probably favoured by *P. antiquata* in the past.

CONCLUSIONS

The discovery of *Praecaryodes antiquata* in the sediments of the Rundle Formation has important implications for understanding the evolution of the Caryodidae in eastern Australia. Shell features of this taxon indicate early diversification of the family on the Australian land mass which rivals the appearance of the camaenids in Laurasia. Climatic change since the Miocene not only led to the extinction of *P. antiquata* but also profoundly affected the evolution of the family which displays a preference for moist forests. The colonisation of the eastern Australian rainforests by camaenids from the Papua New Guinean region most likely usurped the adaptive zone (microhabitat) previously held by *Praecaryodes*.

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